ÖGH Herpetozoa
Austrian Herpetological Society

Herpetozoa 36: 53–58 (2023)
DOI 10.3897/herpetozoa.36.e98931

Body size and body condition in the nose-horned viper (*Vipera ammodytes*): effects of sex and populations

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https://zoobank.org/59B15D27-0CB6-4945-9A19-0DC825852E30

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Academic editor: Yurii Kornilev ♦ **Received** 16 December 2022 ♦ **Accepted** 26 February 2023 ♦ **Published** 20 March 2023

Abstract

Snakes are ecologically and morphologically plastic organisms that exhibit extensive variations in body size and body condition in response to environmental factors. Documenting inter-population variations is important to describe species comprehensively across their distribution range and to monitor trends over time (e.g. decreasing body condition due to alteration of habitat). Thus, we analyzed the influence of population and sex on body size and body condition in three populations of nose-horned vipers (*Vipera ammodytes*) in Serbia. In one population, males were larger than females ($F_{1,39}$=4.802, p=0.034), but not in the two other populations ($F_{1,36}$=0.075, p=0.786; $F_{1,21}$=0.018, p=0.893). Females exhibited higher body condition (residual values from the regression of log-body mass against log-body size) than males ($F_{1,90}$=10.444, p=0.002); this sex difference was not found in one population when analyzed separately ($F_{1,35}$=1.834, p=0.184). Moreover, we found strong inter-population differences in mean body size and mean body condition ($F_{2,96}$=8.822, p<0.001 and $F_{2,90}$=10.319, p=0.001, respectively). While inter-population difference in body size was driven by males, inter-population difference in body condition was driven by females. These results suggest that, in this species, body size might be an important determinant of mating success in males, while body condition may play a major role in female fecundity.

Key Words

inter-population difference, morphological traits, sexual dimorphism, Viperidae

Introduction

Body size is a central phenotypic trait for most organisms (LaBarbera 1989). In snakes, indeterminate growth means that body size after maturity can be influenced by environmental factors such as food availability; this trait is thus subjected to significant inter-population variation (Madsen and Shine 2000; Aubret 2012). Body condition (body mass scaled by body size) is another key phenotypic trait that affects reproductive success in snakes (Naulleau and Bonnet 1996; Reading 2004). Body condition also responds to environmental variables such as trace metal contamination or climate change (Brischoux et al. 2012; Lettoof et al. 2022). By definition, body size and body condition are uncorrelated (Bonnet et al. 2001). However, in terms of physiology these two traits are not independent (Stearns 1992). Indeed, trophic resources are limited, thus growth in stature trade-offs against body condition increases (Stearns 1992). Overall, complex interactions between environmental factors, sexual dimorphism, reproductive strategies and trophic ecology affect body size and body condition in snakes (Bonnet et al. 2001, 2002; Aubret et al. 2002; King 2002; Beaupre 2008; Zuffi et al. 2010).

We studied body size and body condition in free-ranging nose-horned vipers (*Vipera ammodytes)* from three

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widely separated populations in Serbia. Because environmental factors are likely to vary among sites (populations), differences in body size and body condition were expected. We also considered sex, because in this snake species, males tend to attain larger body size than females (Tomović et al. 2022).

Methods

Study species

Vipera ammodytes is a venomous viper distributed in Europe and Asia Minor (Agasyan et al. 2009). In Europe, it inhabits southern Austria, northern Italy, and the Balkan Peninsula (Crnobrnja-Isailović and Haxhiu 1997). Preferred habitats of this species are xerothermic rocky places with shrubby vegetation cover, but nose-horned vipers can also be found in sparse forests and man-made stone walls (Agasyan et al. 2009). *Vipera ammodytes* displays sexual dimorphism in tail length with males having longer tails, more subcaudal scales and larger body size, while females have wider ventral scales (Tomović et al. 2002, 2022).

Study sites and data sampling

The three study sites were located in Serbia (Fig. 1): 1) Natural Monument Lazarev Canyon (**LC**) is a protected area located in Eastern Serbia (about 440 m a.s.l.). The rocky canyon is covered by dry deciduous forest. 2) Svilajnac surroundings (**SV**) is situated in Central Serbia (about 100 m a.s.l.) near the Velika Morava River and near the town of Svilajnac; habitats include deciduous forest, shrubs, and arable land. In this locality nose-horned vipers have been harvested for venom extraction since 1990s (Čubrić and Crnobrnja-Isailović 2022). 3) The Ibar River Gorge (**IR**) is situated in the central part of Serbia (270 m a.s.l.). In this rocky gorge, sparse vegetation cover includes shrubs and patches of deciduous forest.

In each of the three locations, we (TČ for all three populations, TČ and JC-I (for 2 field trips) for SV and IR populations) visually searched vipers from 10:00h to 18:00h along two standard transects of approximately the same length (4000 m). Searching was performed over approximately five consecutive days (±2 d) per season (spring (April-May), summer (June-August), autumn (September-October)) per locality. IR and SV were monitored from 2016 to 2020 (roughly 70 days), LC in 2018 and 2019 (roughly 40 days).

We captured snakes by hand. We measured snout to vent length (**SVL**) and total length (**TL**) to the closest mm using plastic meter tape (precision 1 mm). Body mass (**BM**) was recorded using a spring scale (±5 g). Sex was determined in juveniles and adults by palpation of hemipenes (neonates with 17.8<SVL<25.0 cm were not sexed and were discarded from analyses). We calculated Body Condition as the residual values from the linear regression between Log-BM against Log-SVL; therefore, body condition was not correlated with body size, by definition (Bonnet et al. 2001). Vipers were marked individually by scale clipping and every animal was photographed. We did not include the recaptures in the analysis. We performed all measurements *in situ* and the vipers were released immediately after processing. To count for observer's bias, all measurements were done by the first author.

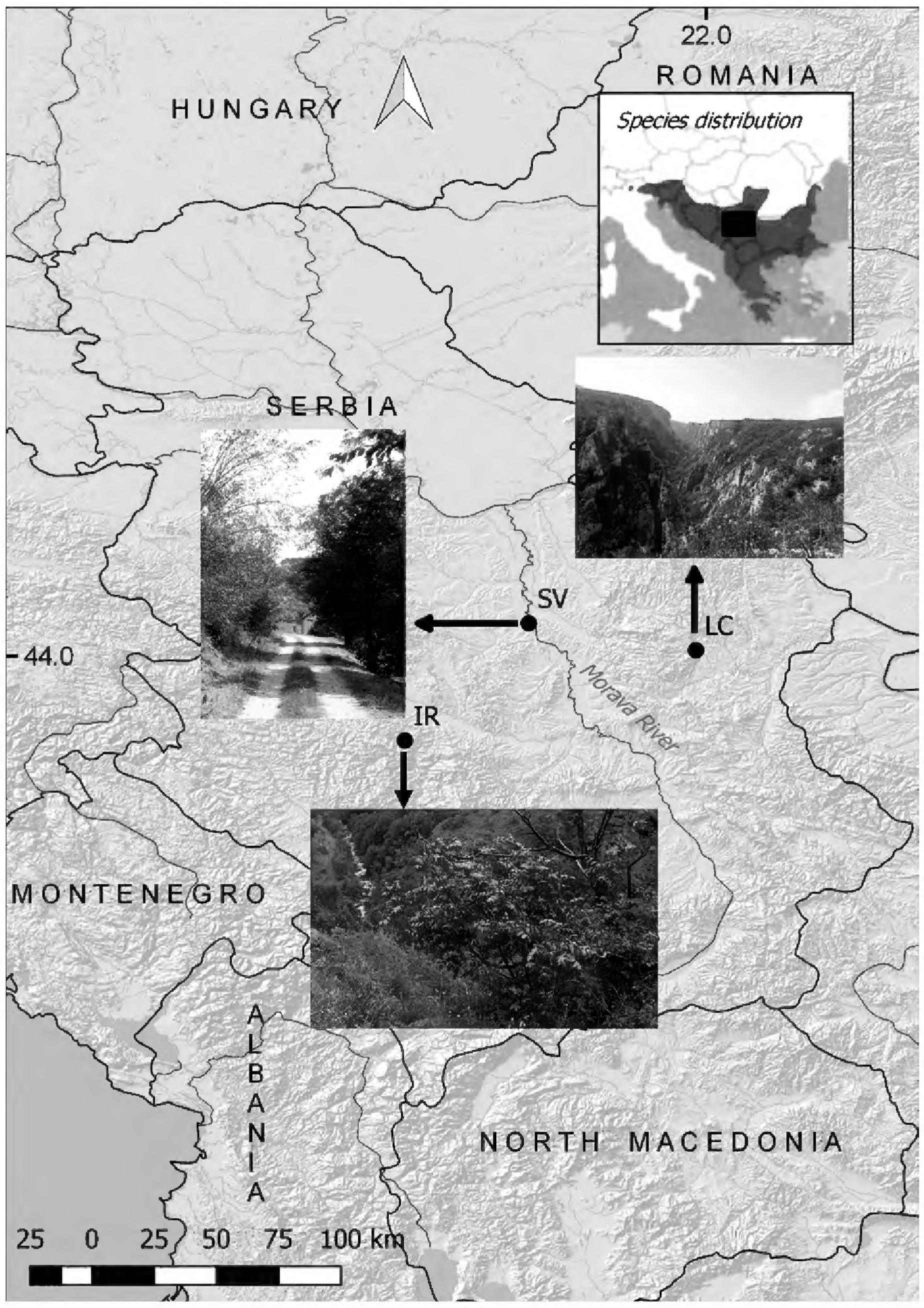

Figure 1. Indicative locations of the studied populations. Three sites were monitored: Lazarev Canyon (LC), Ibar River Gorge (IR) and Svilajnac surroundings (SV). The photographs inserted illustrate the type of habitat (photographs by T. Čubrić).

Vipers have been and still are, in some parts of Serbia, illegally killed and collected for venom extraction and possibly pet trade (Čubrić and Crnobrnja-Isailović 2022). Therefore, we do not provide the exact GPS coordinates of the populations (Console et al. 2020). Indicative locations of the studied populations are shown in Fig. 1.

Statistical analyses

Each individual was represented only once in the analyses and only data from the first capture were used. Data were Ln transformed prior to analyses. Body measurements were analyzed using ANOVA and General Linear

Model (**GLM**). Measuring body size and body condition is relatively straightforward in elongated and limbless animals such as snakes; SVL and BM provide major descriptors of individual's morphology. Nonetheless, body condition does not merely correlate with fat stores, thus its meaning should be interpreted with care (Weatherhead and Brown 1996). In this study, snakes were not fully palpated in order to limit disturbance; body condition calculation included vitellogenic and gravid females along with individuals with food in the gut. Thus, different elements (e.g., body fat reserves, follicles, prey remains) contributed to body condition; but all of them were positively associated with food intake, thereby reflecting local food availability. Analyses were also performed separately for each population to examine more finely possible sex effect (thus, the population effect on the total variance was diminished). Parturition occurs in late summer, provoking a sudden drop in female body mass. Restricting analyses to spring (or spring and summer) did not change the patterns, but several results became marginally significant due to the loss in statistical power. This suggests that post parturition drop of body mass did not alter the observed trends. Consequently, we retained the three seasons during analyses. Statistical tests were performed using STATISTICA 7.0.

Results

Table 1 provides an overview of the number of snakes sampled in each population. The initial total sample consisted of 128 individuals – 37 from LC, 53 from SV and 38 from IR). However, as we discarded snakes with SVL of less than 25cm for analyses, several BM were not recorded; the resulting sample size was of 102 vipers.

Body size and body mass

The smallest male was from IR (SVL 29.5 cm, TL 33.0 cm) and the largest was from SV (SVL 69.8 cm, TL 80.0 cm). BM ranged from 20 g in LC to 220 g in SV. Both the smallest and the largest female were from LC (SVL 26.5 cm, TL 30.7 cm and SVL 60.0 cm, TL 67 cm, respectively), while BM ranged from 20 g to 165 g, respectively (Table 1).

Table 1. Body size and body mass (mean±SE) in three populations of nose-horned vipers surveyed in Serbia. LC stands for Lazarev Canyon, SV for Svilajnac surroundings and IR for Ibar River Gorge.

Population	Sex	N	SVL	BM
LC	males	11	45.22±2.79	69.54±10.28
	females	12	45.35±3.40	87.91±14.45
SV	males	28	55.21±1.48	110.51±11.48
	females	13	50.66±1.41	114.00±6.60
IR	males	23	44.86±1.24	74.77±5.28
	females	15	43.44±1.48	72.69±3.86

We found a strong effect of population on SVL (ANOVA with Ln-SVL as the dependent variable and sex and population as the factors: $F_{2, 96}$=8.822, p<0.001), but no effect of sex ($F_{1, 96}$=1.614, p=0.207) and no interaction between population and sex ($F_{2, 96}$=0.914, p=0.404). SV vipers (both sexes pooled) were larger (52.9±8.2 [SD], N=41) than LC (45.3±10.4, N=23) and IR vipers (43.8±6.0, N=38). Body mass was highly correlated to SVL (r=0.870, $F_{1, 100}$=311.83, p<0.001); similar results were obtained using BM instead of SVL (strong population effect without effect of sex). SV males tended to be larger than the females, but this effect was detected only when SVL was analyzed specifically in this population ($F_{1, 39}$=4.802, p=0.034) (Table 2). However, BM did not differ between sexes in SV population ($F_{1, 39}$=0.016, p=0.900). Similarly, no sex differences were found in the two other populations when analyzed separately.

Body condition

Body condition (GLM with Ln-BM as the dependent variable, sex and population as the factors and Ln SVL as covariate) was influenced by sex and population without interaction between these factors (Table 3, Fig. 3). Mean body condition was higher in females (Fig. 2) and in SV population ($F_{1,90}$=10.444, p=0.002; $F_{2,90}$=10.319, p=0.001 respectively). When conducted separately for each population (Table 2, Fig. 3), significant sex effects were found in SV and LC where females exhibited higher body condition than males ($F_{1, 38}$=11.528, p=0.002 and $F_{1, 20}$=6.203, p=0.023 respectively), but not in IR ($F_{1, 35}$=1.834, p=0.184) (Table 2, Fig. 3) .

Table 2. Effect of sex on body size and body condition analyzed separately for each of the three populations. Significant effects are in bold.

Population	SVL		Body condition	
	F	*p*	*F*	*p*
SV	4.80	**0.034**	11.52	**0.002**
IR	0.075	0.786	1.83	0.184
LC	0.018	0.893	6.20	**0.023**

Table 3. Results from a GLM with Ln-BM as the dependent variable and sex and population as the factors and Ln-SVL as covariate. Body condition was significantly influenced by sex and population without interaction between these factors. Significant effects are bolded.

Effect	SS	Df	*F*	*p*
Intercept	1.505	1	38.958	**>0.001**
Ln-SVL	9.243	1	239.322	**>0.001**
Sex	0.403	1	10.444	**0.002**
Population	0.797	2	10.319	**>0.001**
sex*ln SVL	0.355	1	9.180	**0.003**
population*ln SVL	0.757	2	9.800	**>0.001**
sex*population*ln SVL	0.211	2	2.732	0.070
sex*population	0.214	2	2.770	0.068
Error	3.476	90		

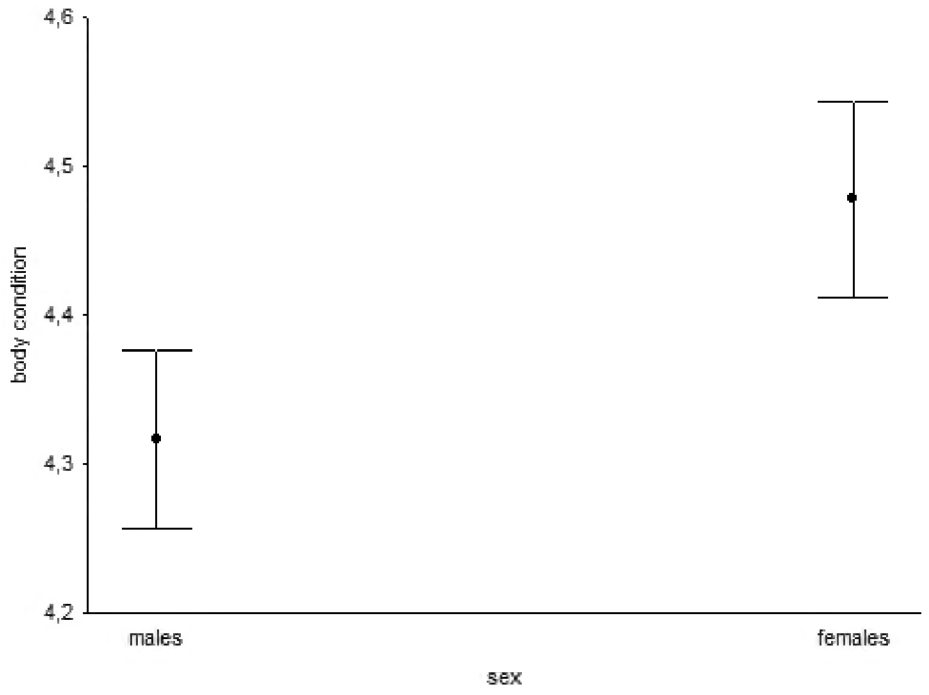

Figure 2. Comparison of body condition between sexes (all populations pooled).

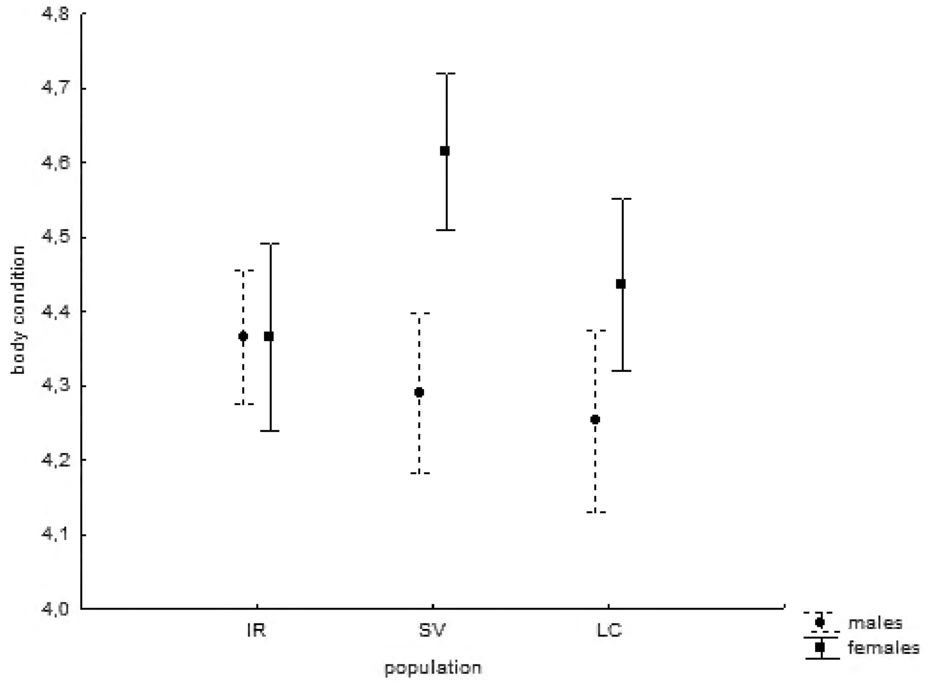

Figure 3. Comparison of body condition between sexes and among populations.

Discussion

We found both sex and population effects on mean body size and mean body condition of *V. ammodytes* studied in three different sites in Serbia, suggesting a role for local conditions such as food availability on growth and body reserve storage. Svilajnac (SV) population hosts the largest and relatively heaviest individuals. This population has been subjected to hunting for venom supply; snake collectors may have targeted a healthy or easily accessible population. Rodents, the main prey of nose horned vipers, are favored by traditional agriculture that creates semi-open habitats with many hedgerows and abundant grass and foraging resources. Such landscapes and fragmented woods persist in SV. Vipers can thrive in peri-urban context provided that favorable partly open bushy habitats are available (Bonnet et al. 2016). The two other populations (Lazarev Canyon, Ibar River Gorge) are situated in markedly less disturbed rocky habitats where lizards are abundant. Smaller body size and lower mean body condition indicate that food availability and prey quality (lizards are less beneficial food items for vipers than micromammals; Zuffi et al. 2010; Tomović et al. 2022) might be lower compared to SV traditional agriculture landscape.

Besides broad geographic patterns, sex differences revealed complex pattern. Both males and females from SV were larger compared to other populations; but this effect was essentially driven by the large SV males (restricting population comparison to males, $F_{2, 58}$=8.675, p<0.001), rather than females (restricting population comparison to females, $F_{2, 38}$=2.834, p=0.071). Consequently, sexual size dimorphism (SSD) was detected only in SV vipers. This outcome mirrors the results from previous studies documenting a lack of, or a significant SSD with larger males in the nose horned viper depending upon study sites (Tomović et al. 2002, 2022; Mebert et al. 2017). Body condition results did not fully match those obtained with SVL. Indeed, in this case females were the main driver of population differences. SV females were in better condition compared to the two other populations (restricting population comparison to females, $F_{2, 35}$=14.381, p<0.0001) while no difference was found in males (restricting population comparison to males, $F_{2, 55}$=1.926, p=0.155; in fact, IR males exhibited the highest body condition). Overall, in the population that may benefit from high food availability, males invest resources in stature growth and females in body reserve storage (plus vitellogenesis) resulting in marked sexual dimorphism in body size (larger males) and body condition (relatively heavier females). In areas characterized by lower food availability, both growth and reserve storage might be strongly constrained, resulting in attenuated sexual dimorphism.

The positive influence of body size on male reproductive success versus the positive influence of body condition on female fecundity has been documented in vipers. Larger male adders (*V. berus*) are more likely to defeat smaller rivals and to court successfully females (Madsen et al. 1993). In the asp viper (*V. aspis*) females need to reach a body condition threshold (meaning that they need to accumulate enough energy reserves) to be able to reproduce (Naulleau and Bonnet 1996). A similar role for body reserves was suggested in the nose horned viper (Luiselli and Zuffi 2002; Phelps 2007). Moreover, body condition positively correlates with fecundity in the aspic viper (Bonnet et al. 2001). The notion that males may benefit from the allocation of resources into growth while females' reproductive success should be enhanced by the allocation of resources into body reserves and vitellogenesis might be general in snakes (Shine 2003).

Although body size and body condition are highly plastic traits in snakes (Bonnet et al. 2021), we cannot exclude the possible role of local genetic adaptation (King and Lawson 2001). Čubrić et al. (2019) identified two overlapping genetic clades of *Vipera ammodytes* in SV region, while in IR and LC only one clade was found. Genetic investigations are required to clarify this issue.

Conservation issues

Habitat loss, climate change, contamination, over-collection for venom supply and illegal pet trade represent a cocktail of threats for the nose-horned viper, but the

IUCN Least Concern species status could make it rather unattractive for conservation funding agencies (Čubrić and Crnobrnja-Isailović 2022). Therefore, monitoring of the nose-horned viper populations is essential to prevent silent declines. Our data contribute to the establishment of a landmark for long-term population monitoring. In this endeavor, the complex interactions between habitat, local environmental conditions and sex on body size and body condition in this species must be considered.

Acknowledgements

We are grateful to Yurii Kornilev and to anonymous reviewers for the useful comments and suggestions that improved the quality of this manuscript. The fieldwork was funded by The Rufford Foundation (grants no: 19578-1 and 23392-2) for TČ. TČ and JCI were also supported by the Ministry of Education, Science and Technological Development of Republic of Serbia – contracts no. 173025 (2016–2019), 451-03-68/2020-14/200124 (2020), 451-03-9/2021-14/200124 (2021), 451-03-68/2022-14/200124 (2022) and 451-03-47/2023-01/200124 (2023). JCI was additionally funded by the Ministry of Education, Science and Technological Development of Republic of Serbia – contracts no. 451-03-68/2020-14/200007 (2020), 451-03-9/2021-14/200007 (2021), 451-03-68/2022-14/200007 (2022) and 451-03-47/2023-01/200007 (2023). Permits for handling vipers and for entering protected areas were issued by the Ministry of Agriculture and Nature Protection (No. 353-01-170/2016-17 for 2016, No. 353-01-2666/2016-17 for 2017, No. 353-01-1359/2017-04 for 2018, No. 353-01-2892/2018-04 for 2019. and 021-01-5/11-1/2017-09 for 2020).

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